EXPERIMENTAL STUDIES OF THE SPECIES CONCEPT

BY EDGAR ANDERSON
Missouri Botanical Garden, St. Louis

This review is dedicated to Dr. J. M. Greenman, former Curator of the Missouri Botanical Garden Herbarium and my colleague during much of the time these studies got underway. In answering my naive questions about the species problem, he frequently quoted to me the statement "Species are but judgments." It was due to him that I became fascinated with the problem of finding factual evidence as to the ways in which such judgments are formed.

Figure 1 illustrates two extreme uses of the word SPECIES in discussions of the species problem. Such discussions are often at cross purposes because those participating are unaware of these differences.

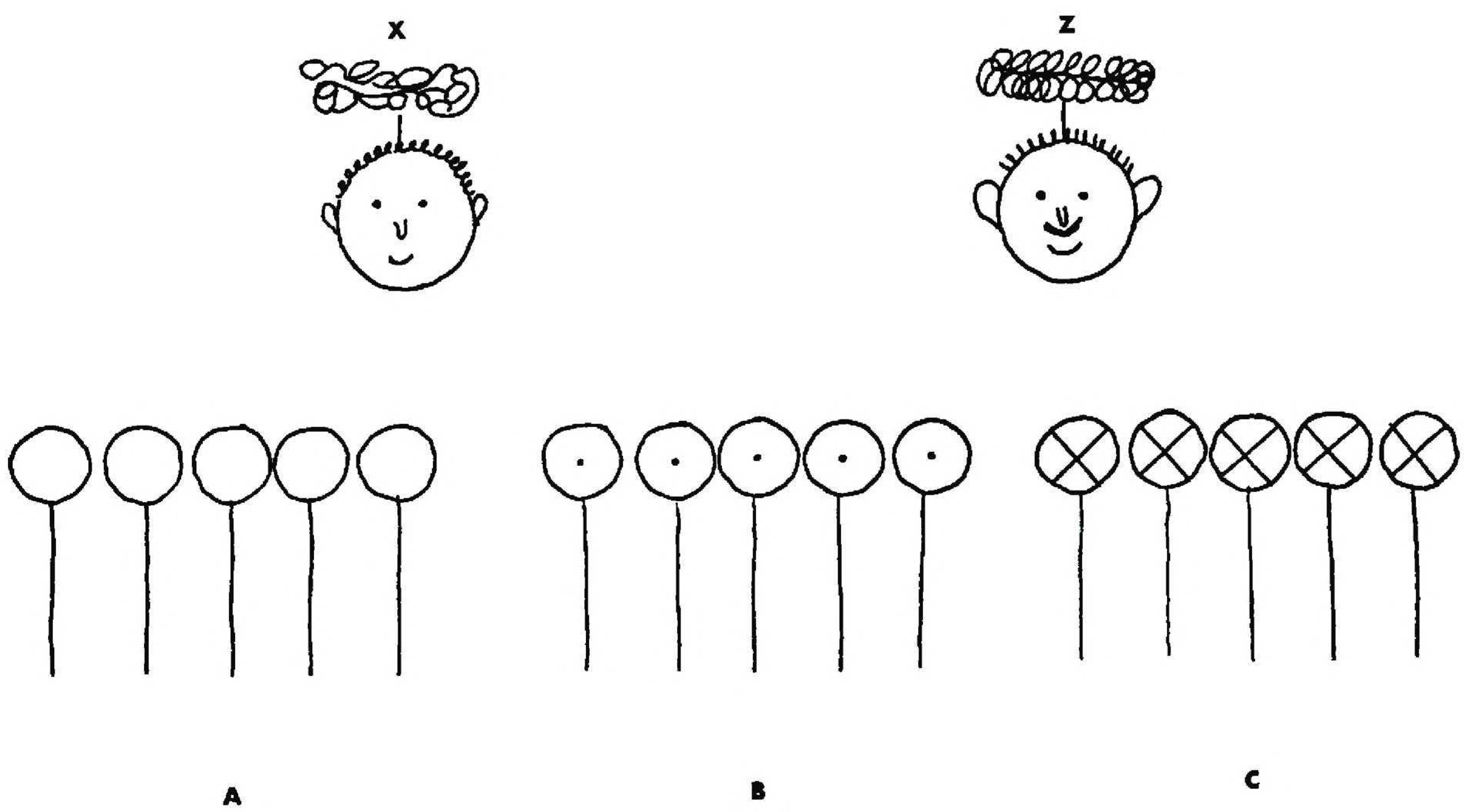

Fig. 1. Diagram of two extreme uses of the word Species.

The diagram shows three taxa of one genus, they may be species, subspecies, or formae but each of the three is represented by individual plants or animals which have certain features in common. This is symbolized in the diagram by 5 individuals of taxon A with no markings, 5 of taxon B with dots and 5 of taxon C with crosses. At the top of the figure are symbolic representations of two gentlemen, Mr. X and Mr. Z, each of whom has been studying the 15 specimens. Above Mr. X's head is symbolized his concept of the taxonomic relationship of A, B, and C. Mr. Z's concept is diagrammed in a similar manner. The diagram would be exactly the same if the two men were in perfect agreement as to the classification of the 15 specimens or if they disagreed in part, or completely. Mr. X, for example, might feel that A with no markings should be species A, and that B and C were

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differing forms of that species. Mr. Z might think that all the differences among the 15 specimens were too minor for taxonomic recognition. In any such example, however, in discussions between Mr. X and Mr. Z, the word "species" might (1) be referring to groupings of the individual specimens of A, B, and C which merited recognition as species or (2) the word "species" might be equated to the concepts X and Z which had matured in the minds of the two men and in which examinations of A, B and C might or might not have played a part.

These matters are well known to most authorities on the species problem. Few of them have made experimental analyses of the species as a concept, but these prejudices are now breaking down rapidly.

Eight such papers were published between 1954 and 1966. They are reviewed below in the order in which they were published. In quoting from those papers of which I was one of the authors, the original text has been shortened but in no case has the sense been changed, though slight differences in shades of meaning are unavoidable in radical condensations.

(1) Speciation in *Uvularia*, by Edgar Anderson & T. W. Whitaker (1934). This paper was (pp. 30-31) "an attempt to present objectively in a codified form the essential facts as to resemblances and differences within and between two similar but distinct species; to reproduce in a concise manner for non-taxonomists the kind of data which are consciously or unconsciously used by taxonomists in the delimitation of species. If a species cannot as yet be defined in terms that are meaningful to workers in other fields, one can present the range of variation within and between two closely-related species in a summarized form for non-taxonomists.

"*It is not a taxonomic thesis.* The two species were chosen for study because there was general agreement that they were specifically distinct from one another and were closely related species of one genus." By diagrams to scale, objective evidence was presented that *Uvularia perfoliata* and *U. grandiflora* had four measurable differences in the leaves, five in the nodes of the stem and inflorescence and four in the flowers. Of all these, only three were discontinuous; the acknowledged discontinuity between the two species is "a discontinuity of combinations reinforced by a few truly discontinuous differences."

It does not seem to be generally realized that species may be, and customarily are, thought of in different ways by different groups of biologists. Biologists engaged in taxonomic work will think of species in terms of the precise differences that permit their ready classification; that make it possible to arrange species in an herbarium or to construct a key to a genus. To them the essential differences between these two species of *Uvularia* will be those few discontinuous ones that are ordinarily used in identifying the species.

"With this attitude we have no quarrel, recognizing systematics as a difficult and necessary business and that those who have it in hand must be allowed to develop their own methods. Yet there *are* those who are interested in the biological makeup of the units which are being classified. This group will include some taxonomists; the separation of the two kinds of thought is not absolute. To us the difference between two species is the difference between one kind of germplasm and another. As geneticists we have gained an impression of two different life-stuffs, each of which reacts variously with the environment. Individual plants produced cooperatively by the germplasm and the environment will show only one facet of that germplasm. For the full expression of a particular species there will be required a series of individuals produced under various environments."

In presenting evidence for differences between the two species of *Uvularia* in their branching patterns and leaf shapes and in the internode patterns of their stems, a combination of measurements and standardized glyphs was used (p. 32). These were developed into a series of charts for graduate classes and lectures at symposia and for the general public. They are discussed below in reviewing the fifth paper.

The first paper in the field of this review presents little objective evidence about the concepts in the minds of systematists, but the diagrams (Fig. 1) do analyze the kinds of evidence that are before ones eyes when working in an herbarium, a museum, or an experimental plot. Taxonomists certainly differ greatly in their ability to form useful "judgments" from such subtle data as trends in shape. Greater skill in that direction is probably responsible for the "taxonomic intuition" of such taxonomists as George Engelmann. His judgments about the classification of western American plants were derived mostly from tiny scraps of material, but they have stood the test of time.

(2) An experimental study of hybridization in the genus *Apocynum*, by Edgar Anderson (1936).

In his Doctor's thesis my colleague Dr. Robert E. Woodson published an interpretation of the phylogeny of the genus *Apocynum* which was decades ahead of its time. He envisaged it as a genus in which inter-specific hybridization has been so important that its evolutionary pattern is more like an anastomosing network than a branching tree. To me his ideas "though stimulating and interesting, seemed rather in need of experimental confirmation by other than purely morphological criteria. After much friendly argument an experiment was planned," a simple progeny test of two common American species, *Apocynum cannabinum* and *A. androsaemifolium*, strikingly different plants, and their putative hybrid, *Apocynum medium*. Woodson gathered seed from several different plants at a site in Indiana where all three species grew near one another, and I made supplemental collections in New England. I supervised raising the seedlings to flowering age, scoring pollen fertility, photographing the flowers and making herbarium specimens of each mature flowering plant (Fig. 2).

Since I was then working in Boston and Woodson in St. Louis, it was easy to get precise, objective data on his concepts of speciation in *Apocynum* from his labels on the 40 reticulately-related *Apocynum* specimens I sent him. They had all been collected the same day and were tagged with a randomized set of numbers, the only key to which was in my record book. Woodson had no way of knowing how the specimens fitted together to make 8 progeny tests until I sent him a

Table 1. Progeny tests of one plant of *A. cannabinum* (can), one of *A. androsaemifolium* (and) and five of *A. medium* (med).

Parent Plant	Seedling Number	Identification	Remarks
can-447	1	*A. cannabinum* var. *cannabinum*	
	2	*A. cannabinum* var. *cannabinum*	
	3	*A. cannabinum* var. *glaberrimum*	
	4	*A. cannabinum* var. *glaberrimum*	
	5	*A. cannabinum* var. *glaberrimum*	
	6	*A. cannabinum* var. *cannabinum*	
	7	*A. cannabinum* var. *cannabinum*	
and-503	2	*A. androsaemifolium*	very typical
	3	*A. androsaemifolium*	
	4	*A. androsaemifolium*	fairly typical
	5	*A. androsaemifolium*	
	6	*A. androsaemifolium*	essentially typical
	7	*A. androsaemifolium*	very typical
	8		
	10	*A. androsaemifolium*	
	Nos. 1 and 9 were lost before their determinations were recorded		
med-446	1	*A. medium*	glabrous leaves
	2	*A. medium?*	like a small *androsaemifolium*
	3	*A. medium*	glabrous
	4	*A. medium*	close to var. *leuco-neuron*
	5	*A. medium*	sparsely pubescent
	8	*A. medium*	glabrous
	9	*A. medium*	glabrous
	10	*A. medium*	unusually small flowers
	11	*A. cannabinum* var. *glaberrimum*	
med-448	1	Probably a glabrous *A. medium*	
	2	*A. medium*	
med-449	1	*A. medium*	but very small flowers
	2	*A. medium*	quite typical
	3	*A. medium*	but nearly glabrous
	4	*A. androsaemifolium*	
	5	*A. medium*	
med-502	1	*A. cannabinum var. glaberimum?*	
	2	*A. androsaemifolium?*	but small flowers
med-504	1	*A. medium?*	
	2	*A. androsaemifolium?*	possibly a hybrid
	3	*A. medium*	
	4	*A. androsaemifolium*	
	5	*A. androsaemifolium?*	corolla rather small

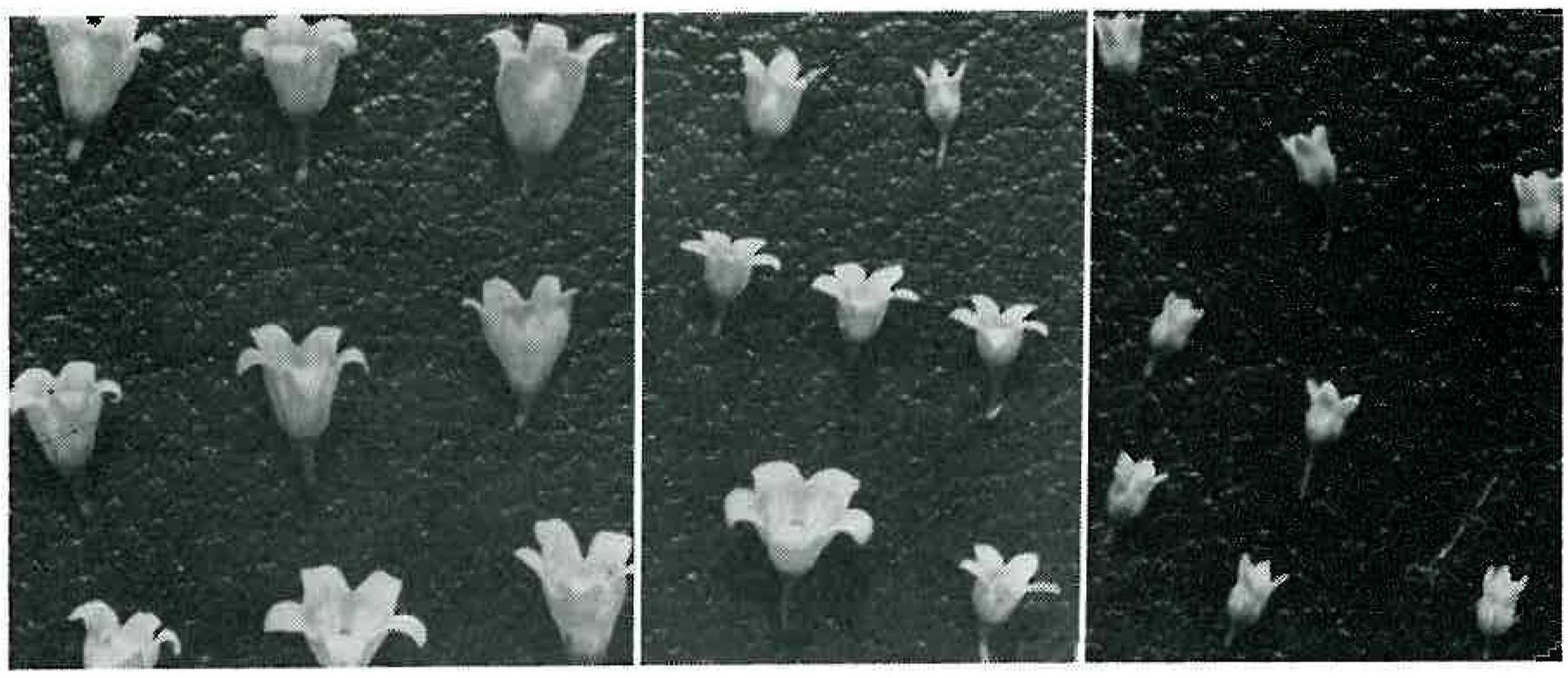

Fig. 2. Progeny tests of three species of *Apocynum*. Each flower was chosen as representative for one plant, all × ½. Left, *A. androsaemifolium;* Center, *A. medium;* Right, *A. cannabinum.*

rough copy of the information in Table 1. It confirmed all his hypotheses, including some I had been skeptical about.

Table 1 demonstrates that all the 6 aberrant specimens that he labelled with questions marks, as well as all the 13 which were so variant that he added informal comments to the label, were seedlings of *A. medium,* the supposed hybrid, thus indicating it to be of hybrid ancestry. Table 1 also presents evidence for a phenomenon that I do not remember having talked, read or thought about up to that time, the various restrictions to free recombination of multiple-factor characters which operate in hybrid germ plasms. The total effect of these restrictions in *Apocynum* is so strong that two *A. medium* seedlings, 449-4 and 504-4 were labelled by Woodson as unquestioned *A. androsaemifolium* and one, 446-11 as unquestioned *A. cannabinum* var. *glaberrimum!* The paper concluded by suggesting that "the chief effect of hybridization in this genus in eastern North America at the present time is to increase variability in the parental species."

It was these experiments with *Apocynum* which lead me to examine the general restrictions to recombination in multiple factor characters and eventually to describe, define and diagram introgressive hybridization.

(3) The Concept of the genus II. A survey of modern opinion, by Edgar Anderson (1940).

From discussions with my colleague Jesse M. Greenman and our students, I became increasingly interested in species as a concept. I sensed that there might be a "Genus Problem" as well as a species problem. Accordingly, when a national symposium on Genera was organized in 1938, I sent out a questionnaire asking in two different ways a basic question about genera and species. The questionnaire was set up to allow any one of five different answers to the first question and four to the second one and was mailed to 43 taxonomists.

Question 1	*No. of replies*
Genus the more natural unit	26
Species the more natural unit	8
Sometimes one, sometimes the other	11
No opinion	1
Question meaningless	2
Question 2	
Genera originate in the same way as species	31
Genera may originate in a different way	4
Genera may originate in same or in a different way	9
No opinion	4

Forty-two taxonomists responded, so many of them with additional comments that a negative correlation between age of respondent and interest in the symposium could be demonstrated in tabular form (see below).

The replies were more uniform than some of the respondents had expected. Twenty-one of them were identical. This orthodox opinion was that genera, on the average, are more natural groups than species, that they originate in the same way, and that generic differences could be compounded from specific differences.

By dividing the respondent into two groups: one, taxonomists whose experience had been mostly in monographic work, and group two, taxonomists who were not monographers or who had extensive experience in other biological disciplines, this correlation could also be tabulated. Of the monographers, two-thirds were "orthodox"; of the non-monographers less than one-third. However, though I was still under 40 when the questionnaires were mailed out, I felt that the "genus problem" required extensive experience with more than one group of organisms, to answer such questions intelligently. I agreed with Liberty Hyde Bailey when he answered "A fair agreement has been reached as to the limits of genera and the limits of species, without much reference to philosophical considerations. Discussion is likely to be made by persons who have no taxonomic training and the conclusions would be of little practical value." C. W. Weatherby, then the assistant curator of the Gray Herbarium, appended to his answer a short distillation out of his own experiences that has important overtones :

	AGE OF RESPONDENT			
INTEREST OF RESPONDENT	Under 40	40-55	Over 55	Total
Not in sympathy	0	0	2	2
Replied without comment	2	7	7	16
Replied with discussion	6	6	5	17
Replied and expressed interest	12	1	1	14
Total	20	14	15	49

"Taxonomy is only a glorified guess—an attempt to construct a cross-section of the lines of descent in a form intelligible to the human mind. It always contains two variable quantities—the plasticity of organic nature and the differing points of view of the people who work at it. You can generalize successfully, if at all, only by keeping these facts constantly in mind. The only general rule is that there is no general rule. Therein lines the fascination of taxonomy for those who like it. *Each group one tackles presents a fresh and original problem: for each, one has to work out anew the method by which he may best achieve that transforming of confusion into order which is the great satisfaction of pure taxonomy.*"*

When the replies to the questionnaire arrived they were of such interest to taxonomists and other biologists that they were bound and filed in the Missouri Botanical Garden Library. Unfortunately this volume was not put in the locked cases which house the Pre-Linnaean Library and other treasures. It was read so frequently that it became dog-eared. Twenty years later it disappeared from the shelf.

(4) Concordant vs. discordant. Variation in relation to introgressive hybridization, by Edgar Anderson (1951).

The above title is misleading for the purposes of this review. The extensive experimental studies of species concepts reported in the preceding review demonstrated great variation between able biologists in perceiving leaf shape and internode-pattern differences. This paper first presents evidence for the taxonomic validity of these characters. With mathematical precision it then constructs a demonstration of the differences in appearance to be expected between populations of plants in which extensive introgression has or has not taken place. The paper belongs in this review because it presents evidence about the importance of the complex differences it refers to as "trends", as measures of species differences in plants and animals.

All taxonomists tested were aware of leaf-shape differences, though most non-taxonomists were more conscious of size than of shape differences. Correlated changes in size and shape, however, had proved so difficult for them to grasp* that a large half of this paper is a demonstration of that relationship with tracings, diagrams, and discussions.

The first evidence presented is leaf shapes of two common wild cherries of the eastern United States, the choke cherry, *Prunus virginiana* and the rum cherry, *P. serotina*. "The outstanding difference is in the *trend* in proportion. As the leaves of *Prunus virginiana* get longer, they get correspondingly broader. As the leaves of *P. serotina* get longer they get only slightly wider. In *P. serotina*, therefore, the largest leaves are the narrowest, the smallest the broadest; in *P. virginiana* the largest are the broadest, the smallest the narrowest. Such differences in trend of related parts seem to be generally characteristic of specific differences. I found such differences in trend in all the species (of several genera) for which I had made pressed population samples."

Trends in internode patterns became easy to demonstrate and to record precisely by a method originated by a botany major, Dorothy Schregardus. She used it to analyze the growth and development of the common sunflower and it

* Italics added by the reviewer.

* Though many of them apprehended them, apparently instinctively.

was published as Anderson & Schregardus (c), a method for recording and analyzing variations of internode pattern. The internodes of the stem were diagrammed along the horizontal axis at regular intervals from left to right, 1, 2, 3, 4, etc. as in a scatter diagram of correlation. The length of each internode was then diagrammed vertically in centimeters to an appropriate scale, with a dot. The successive dots were connected with straight lines whose slope was a precise record of the rate of increase or decrease from one internode to the next for the internodes of the entire stem. This simple device has been effective in various studies of plant development and in making exact measures of plant-to-plant differences when interpreting the variation of introgressing populations.

Its most extensive use has been in classifying *Zea mays.* Additional symbols were added to these maize-internode diagrams. A solid black circle marked the position of the last internode below the male inflorescence (the "tassel") and a solid black triangle the position of the corn ear, or of each ear in multiple ear varieties and races. Such diagrams, with minor variations, have been used in more graphs on the races of maize in Brazil, Cuba, Colombia, Central America, the West Indies, Chile, Peru, and Bolivia* sponsored by the National Academy of Sciences and the National Research Council. They are proving useful in developing hybrid corn for Latin America and in the tropics and sub-tropics generally. They demonstrate how a concern for understanding the concepts by which taxonomists evaluate differences between species grew into the use of basic physiological differences in classifying economic plants.

(5) Efficient and inefficient methods of measuring specific differences, by Edgar Anderson, (1954).

This reprint from Kempthorne, Bancroft, Gowen and Lush is included because, though it was prepared for an audience of statisticians and mathematicians, it contains the only published evidence of my most extensive experimental investigations of the species as a concept. As in the first paper reviewed, *Uvularia* furnished the research material. "To get at the fundamentals of the species problem, one needs to choose the simplest possible species. *Uvularia grandiflora* and *U. perfoliata* were chosen for demonstration because there has been universal agreement among those who have dealt with them that they are both good species, that they belong to the same genus, and that they present no special problems of classification, distribution or ecology. Both are known to be diploids; there are no indications of other complicating factors. These two species differ in the presence or absence of hairs on the underside of the leaves and by curious glandular outgrowths on the inner face of the perianth in *U. perfoliata* that have no counterpart in *U. grandiflora.*" They also differ by many minor, more-or-less-correlated differences in the size, proportion, texture, number, and arrangement of the various internodes, leaves, and scales that make up the vegetative parts of the plant that

* See for example, Races of maize in Bolivia, Ramírez et al., in collaboration with G. Edward Nicholson Calle, Edgar Anderson, William L. Brown. 1960. Publication 747: Nat. Acad. Sci.—Nat. Res. Council, vii + 159 pp.

are above ground. To analyze the nature of these differences it was necessary to choose a few from among the hundreds of sense impressions coming to us from each plant. The length of every leaf and the length of every internode was recorded, as well as the position of every flower and every scale-leaf (cataphyll). From these measurements and scores, an "ideograph", a sort of diagrammatic skeleton of each specimen, was reconstructed (Fig. 3). The width of the leaf, the angle of branching, the sizes of the flowers, and of the cataphylls at the base of the stem, were all conventionalized. Flowers are represented as black disks, leaves as wide lines but to scale, cataphylls as short narrow lines. The length and number of internodes is indicated by the positions of the leaves and cataphylls. The variation of all these variables was analyzed mathematically. *Uvularia grandiflora* was shown to be "represented by a coherent group of individuals." *Uvularia perfoliata* was not so coherent. Some of the specimens vary in the direction of *U. grandiflora,* suggesting that introgression from that species, previously unsuspected, may be responsible for these variants. These conclusions were confirmed and extended by Dietz (1952).

Experimental studies of the perception of these species-differences were made with reproductions of the 20 ideographs on plain white cards, a little larger than playing cards, or with poster-size enlargements for public lectures. People being tested were usually not told how many species were represented. It was found that biologists differ greatly in ability to separate the two species correctly from these cards and in the speed with which they can do it. At one extreme was a graduate student in comparative anatomy. With no previous experience, he sorted all twenty

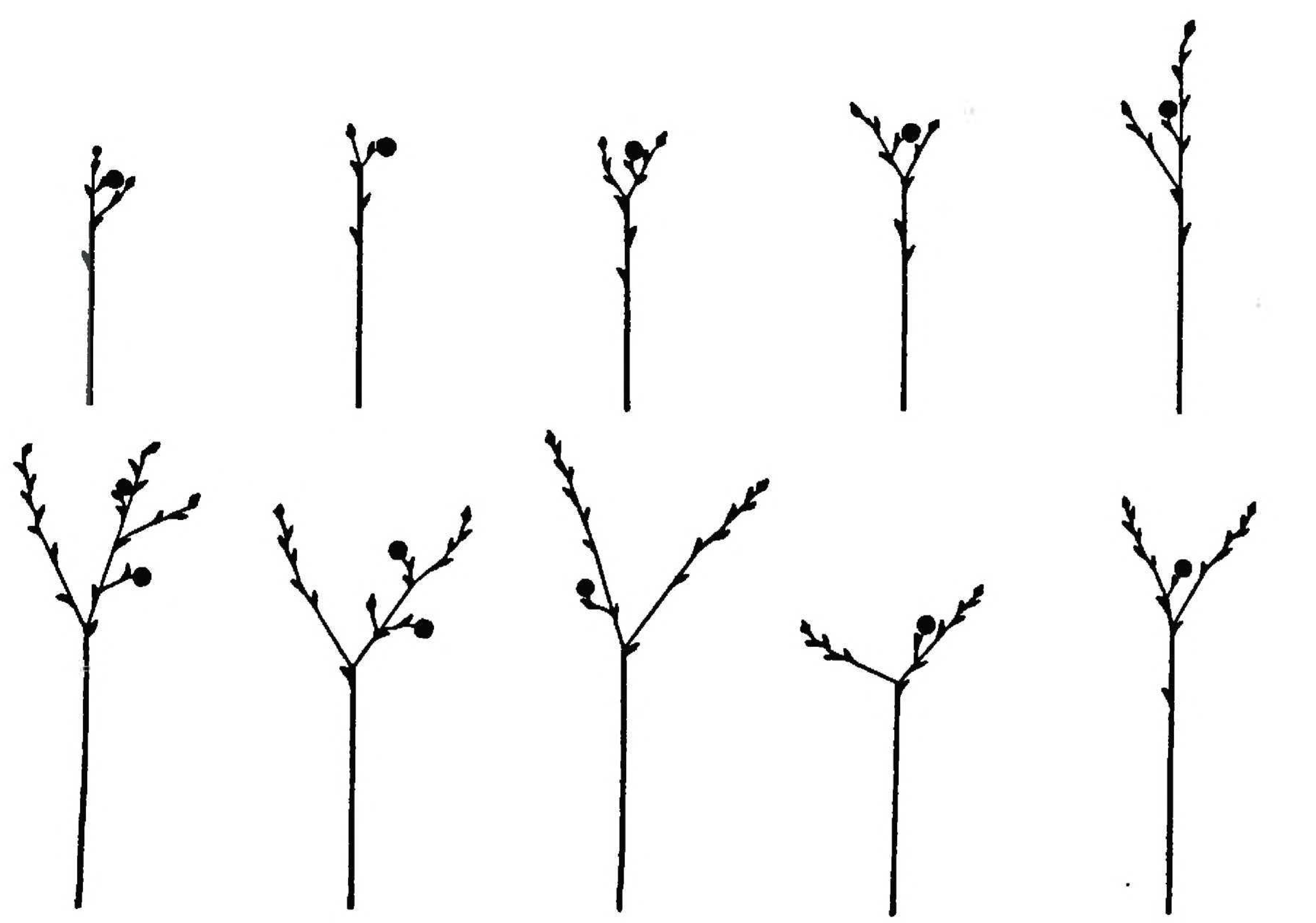

Fig. 3. Ideographs (to scale) of 5 plants each of two species of *Uvularia,* above *U. perfoliata,* below *U. grandiflora.*

out correctly in less than ten minutes. At the other extreme was an able monographer and museum curator. He studied the cards carefully and laid them out in little groups of almost identical ideographs. One or two of these he was able to unite, but most of his units he placed halfway between two others until the whole table-top was covered with a complex web-like arrangement of little groups of cards. He was intrigued by the challenge and kept at the problem intermittently for hours with no success. I suspect that he had more of the basic facts about each specimen in his mind than anyone else I ever tested, but that he had no instinctive way of ignoring maturity differences when looking for specific differences. I suspect also that he was not facile in apprehending differences in internode patterns. When the method of diagramming internode patterns described in the following review was adapted to the *Uvularia* ideographs, it produced diagrams which were easier for students to classify correctly.

From testing students with these ideographs, and from observing taxonomists at work, I believe that there are innate differences between people in their ability to apprehend significant clusters of variables as indicators for malnutrition, maturity, specific differences, etc. Some of those most highly endowed are unaware that they have exceptional gifts in that direction. Able scientists with little of this ability can be helped by a good teacher. Some able taxonomists with little of it, and that little not well-developed, are prejudiced in appraising the work of those who are highly endowed.

(6) An analysis of variation in a variable population of *Cladonia*, by Edgar Anderson and E. D. Rudolph (1956).

This analysis of introgression between species of two lichens is included in these reviews because the same specimens studied by the authors were sent to an authority on *Cladonia*, identified only by numbers, for precise identification. His groupings of the specimens and the authors' are in close agreement. The authors' groupings confirm the generalization of the second review that one of the important results of hybridization is enrichment of variation in the parental species. The contrast between his concept of speciation and their approach to the problem is shown in detail in Figs. 7 and 8. They demonstrate his concepts as well adapted to cataloguing such a hybrid swarm, and the authors' as adapted to analyzing its evolutionary dynamics. This also justifies the paper's introductory remark "that populations which suggest hybridization to the experienced eye have much the same variation pattern as back-crosses of experimentally produced hybrids."

More than any other study of introgression this paper shows step by step how precise measures were worked out for analyzing the variation. The methods adapted for measuring potential variation, demonstrated in figures one to four, could probably be adapted to various kinds of non-vascular plants.

(7) An experimental investigation of judgments concerning genera and species, by Edgar Anderson (1957).

Having learned (No. 3 above) that taxonomists agree in their judgments of species and genera more than they realize, I gathered objective evidence about concepts of species and genera by a simple method. I compared the assignments to species and genera made in two rival floras dealing with the vegetation of the eastern United States. From Fernald's last revision of Gray's Manual and Gleason's New Britton and Brown Illustrated Flora, I made extensive spot checks of their agreement or disagreement in various families and genera. For areas which they both cover they agree at least eight or nine times out of ten. "This is of course a rather limiting case. The flora of eastern North America is relatively stable and it has been well and intensively studied for over a century. In California speciation is much more intricate for all kinds of organisms. Microclimates are much more highly developed. Tertiary and Pleistocene sea-level, rainfall-pattern, and mountain-height changes have been extreme and have led to complicated speciation patterns. The flora furthermore has not been intensively studied for so long a time, yet when one takes two of the standard floras of the state and deals with comparable areas he finds complete agreement 4 to 6 times out of 10 and differences only in detail 2 to 3 times out of 10." Acrimonious disputes between taxonomists have mostly been over the small percentages of instances in which they did not agree.

These concurrences of opinion convinced me that there is a GENUS PROBLEM worth studying as well as a SPECIES PROBLEM. Through the kind offices of Dr. Robert Cooper, 16 specimens of *Uvularia perfoliata* and *U. grandiflora* were studied in turn by three New Zealand systematists who were unacquainted with the North American Flora. None of them had specialized on the *Liliaceae*. All three placed all 16 in the same genus, proving that there is a Genus Problem worthy of extensive study in its own right.

"The central core of the instructions accompanying the sheets was as follows: What I should like is your judgment after examining the specimens as to how many species, varieties, and genera are involved and (by the numbers) how these 16 plants are to be classified. I am not at all interested in having you identify them as to family or genus. Quite the opposite; I hope you will not refer to the literature until after you have dealt with the specimens (if then). This much I can assure you. They were chosen because their classification presents no problems and has never been under dispute. If, for instance, they belong to five species in two genera, then the species are all clear cut and the genera are universally recognized as coherent, distinct genera. If there are any varieties or sub-species present in the material then they too are well-marked variants but not so distinct as to merit specific recognition in the opinion of anyone who has dealt with them."

Note that the recipients were given no clue as to the number of genera, species and varieties included in the sample; they were, if anything, encouraged to believe that more than one genus was involved. They were assured that no problem genera, nor hybrid swarms, nor apomictic groups of doubtful relationship had been included in the sample.

Of the three systematists, one was a distinguished monographer of another family of plants, and he worked independently of the other two. They discussed the specimens with each other but made their final judgments independently. One had carried on extensive field work in biosystematics, the third was an algologist.

The latter separated *U. grandiflora* from *U. perfoliata* but divided each of them into two separate species. It was concluded that there is close agreement among taxonomists on the relation of species to genera even for specialists of different backgrounds and different kinds of training. Their judgments are apparently intuitive and inarticulate. The species-genus relationship deserves coordinated research with biological and psychological techniques.

(8) Folk taxonomies and biological classification, by Brent Berlin, Dennis E. Breedlove and Peter H. Raven (1966).

This short report summarizes the advancing understandings emerging from a remarkable project. It is Science's first accurate, comprehensive attempt to analyze differing concepts of classification in studying the flora of an entire community.

It begins with a refreshingly realistic appraisal of all recent work in this field, and the authors make an exception only for Harold Conklin's Yale dissertation on the Hanuoo culture. "Unfortunately most of the data contributing to our understanding of folk taxonomies are casually collected, non systematic, incomplete and anecdotal."

They concentrated on an area of about 160 square kilometers, the municipio of Tenejapa in Chiapas, Mexico. It ranges from 2700 feet above sea level with legume-evergreen forest in more moist areas, such as along rivers, to mixed pine-oak-sweet-gum forest in the more temperate, middle regions, rising to cloud forest at 9000 feet. "More than 1500 species of vascular plants probably occur in the municipio." From repeated interviews with native informants they believe their sample of more than 1100 plant names in Tzeltal, the native tongue, "is nearing completion."

All their analysis of Tzeltal plant names is based on the "Tzeltal specific" as a unit. They define it as "any taxon which includes no other taxa" and continue "For the purposes of this report we have taken a sample of about 20 percent of our data by including the first 200 Tzeltal-specific names in our alphabetical files. We have no reason to believe that such a procedure biases the results in any significant manner."

For exact comparisons between the taxonomies of Botanical Scientists and the Tzeltal specific names, they divided the latter into three categories, 1) *under-differentiation*, Tzeltal specifics which include two or more botanical species, 2) a one-to-one correspondence and 3) over-differentiation, when more than one Tzeltal specific corresponds to a botanical species. Approximately 41% of the 200 were under-differentiated, 25% were the same and 35% were over-differentiated.

The cultural significance of these Tzeltal specifics to the Tzeltal was graded high, moderate, and low for (1) plants of little or no utility for them, (2) plants of moderate cultural significance, as plants used for fuel or firewood but not cultivated, (3) plants intensively cultivated such as maize, beans, chili peppers and squash, primarily food or cash crops. From these scorings, a strong positive correlation between cultural significance and degree of differentiation was revealed. Forty of the 50 over-differentiated species were judged to be highly significant.

One unexpected result of the analysis was that 40 out of 68 of the plants with a one-to-one correspondence were introduced to Tenejapa after the Spanish conquest. They are invariably used today for the same purposes and in many instances retain their Spanish names.

The authors conclude on a philosophical note, telling us that when we put together such entities as species with the highest proportion of shared attributes, we cannot logically insist that these entities share any one particular attribute. This may tell us little about the structure of nature itself but a great deal about our own view of it!

CONCLUSIONS

During the period that I published the first seven papers of this review, I was increasingly impressed with the importance of joint taxonomic-psychological investigations of the two aspects of the species problem discussed and diagrammed in (1). For none of that time, however, did I have a colleague well-grounded in the fields of psychology pertinent to these studies. The 8th review demonstrates the ways in which such problems could have opened up fruitful new fields of investigation had such collaboration been possible.

Within the last decade I have become aware that experimental investigations of taxonomists' conceptions of taxa *above* the species might produce more effective collaboration of taxonomists with physiologists and biochemists.

When a taxonomic monograph of a group of plants has achieved its goal and put like ones close together that tend to share many common features, it can be widely useful. Taxonomists of the higher plants could be as helpful to biochemistry as were those medical school pharmacologists whose discoveries led to such useful concepts as "psychedelic drugs", in grouping whole sets of compounds together. A very little has already been done. The association of dangerous cyanogens with the *Rosaceae* had long been recognized. See Kingsbury (F) for discussion of this and many other examples.

Various taxonomists are already using biochemical information in classifying plants. The relationship between biochemists and plant taxonomists could become genuine collaboration, profitable to both sciences. Sorbitol, for instance, is common to closely related Asiatic and American species of *Larix* (larch) but is not produced in less closely-related species (reviewer's unpublished information). Such facts are useful not only to monographers of the genus *Larix* but also to chemical manufacturers looking for cheap sources of sorbitol.

Before such a two-way association could become facile, there would have to be a wider understanding among taxonomists as to which sub-genera, genera, sub families and families of higher plants are based on a wide variety of characteristics, each of which is shared by most of the group, in other words is a "natural" group and not an "artificial" one. Various genera, families and higher categories in plant taxonomy are widely recognized as "natural" or "artificial". Taxonomists frequently discuss these matters informally among themselves, but I know of no exposition of the problem except the elementary one cited in (5).

It is becoming widely understood, for instance, that the rose family is a natural group and less widely that one of its sub-divisions, the *Pomoideae*, (the pome fruits—apples, pears, quinces, hawthorns, etc., fruits with a core) are an introgressive, polyploid, apomictic complex whose genera, species and sub-species are artificial. They form such a complex, interwoven network of relationships that there have been wide disagreements between experts in cataloguing them.

No one or two taxonomists could yet compile a working list of outstanding natural and artificial taxa, complete enough to be generally useful. On the other hand, a modern taxonomist, familiar with computer techniques, could organize a survey of present day concepts that could be mechanically sorted. It would, at the very least, be a beginning that would call attention to the problem. It might grow into a catalogue that would be widely helpful.

The closing three paragraphs of the paper by Berlin et al. (8) with a discussion of "general" versus "special" classification, indicate the advances of understanding and of utility to be expected from expert conceptual classifications.

Bibliography

Numbers refer to Papers reviewed; letters to background information.

(1) Anderson, Edgar & Thomas W. Whitaker. 1934. Speciation in *Uvularia.* Jour. Arnold Arb. **15:** 28-42.

(2) Anderson, Edgar. 1936. An experimental study of hybridization in the genus *Apocynum.* Ann. Missouri Bot. Gard. **23:** 159-168.

(A) Anderson, Edgar. 1939. Recombination in species crosses. Genetics **24:** 668-698.

(B) Anderson, Edgar & H. C. Cutler. 1942. Races of *Zea Mays* I: their recognition and classification. Ann. Missouri Bot. Gard. **29:** 69-89.

(3) Anderson, Edgar. 1940. The concept of the genus II. a survey of modern opinion. Bull. Torrey Bot. Club **67:** 363-369.

(C) Anderson, Edgar & Dorothy Schregardus. 1944. A method for recording and analyzing variation in internode pattern. Ann. Missouri Bot. Gard. **31:** 239-247.

(4) Anderson, Edgar. 1951. Concordant vs. discordant variation in relation to introgressive hybridization. Evolution **5:** 133-141.

(D) Dietz, Robert A. 1952. Variation in the perfoliate Uvularias. Ann. Missouri Bot. Gard. **39:** 219-254.

(5) Anderson, Edgar. 1954. Efficient and inefficient methods of measuring specific differences, in Kempthorne, Bancroft, Gowen and Lush. Iowa State College Press, 93-106.

(6) Anderson, Edgar & E. D. Rudolph. 1956. An analysis of variation in a variable population of *Claudonia.* Evolution **10:** 147-156.

(E) Roberts, L. M. et al. 1957. Races of maize in Colombia. Natl. Acad. Sci-Natl. Res. Council Publ. No. 510.

(7) Anderson, Edgar. 1957. An experimental investigation of judgments concerning genera and species. Evolution **11:** 260-262.

(8) Berlin, Brent, Dennis E. Breedlove & Peter H. Raven. 1966. Folk taxonomics and biological classification. Science **154:** 273-275.

(F) Kingsbury, John M. 1965. Deadly harvest; a guide to common poisonous plants. Holt, Rinehart & Winston, N. Y. 128 pp.